HIGH TEMPERATURE EFFECTS ON VEGETATIVE GROWTH AND FLORAL DEVELOPMENT IN *IMPATIENS WALLERANA*

By

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Nineteen cultivars of *Impatiens wallerana* were exposed to day/night temperatures from 18/24 to 34/29°C to evaluate temperature effects on plant growth and flower development. Generally, higher temperatures increased vegetative growth but decreased plant quality and reduced flower size. Variation in heat sensitivity was observed in these 19 cultivars. 'Dazzler White', a heat tolerant and 'Super Elfin (S.E.) Red Velvet', a heat sensitive impatiens cultivar, were selected for further study of high temperature effects. High temperature (39/31°C) reduced flower size and the effect became more significant as exposure time increased from 1 to 8 days. Photosynthetic rates were also inhibited by high temperatures. This inhibition was probably due to non-stomatal effects, because water vapor conductances for both cultivars were not affected by temperature treatments. Temperature increase from 28/20 to 38/30°C caused decreases in leaf and xylem water potentials and a decrease in relative water content (RWC) in petals and leaves. Invertase activity and ^{14}C-assimilate partitioning were affected less by high temperature in 'Dazzler White' than 'S.E. Red Velvet'. High temperature inhibited the partitioning of ^{14}C-assimilate to flower buds and increased the amount recovered from stems in 'S.E. Red Velvet',

At temperatures of 33/25 and 38/30°C, invertase activity in flower buds of 'S.E. Red Velvet' decreased 32 and 45% respectively compared to 28/20°C. With increasing temperature, the levels of sucrose in young flower buds increased while the starch content decreased. As flower buds developed from young to mature, both sucrose level and starch content decreased markedly; there was less effect on sucrose level. Decreases in sucrose and starch were likely providing hexoses for metabolism and biosynthesis. However, the extremely low glucose concentrations found in the flower buds under the highest temperatures probably resulted from excess respiratory depletion of carbohydrate. It appears that the reduction in flower size within 1 or 2 days was due to high temperature induced water stress. The more long term effects were caused by lower levels of soluble sugars and starch. According to these results, careful selection of cultivars during high temperature periods would partly offset heat stress production problems.

CHAPTER 1
INTRODUCTION

Bedding plant production is an important segment of the floriculture industry. The total farm gate value of bedding plants in 1989 was $867 million, which accounted for 36% of reported total floriculture sales at $2.43 billion (United States Department of Agriculture, 1990). As the market continues to expand, more growers are expected to contribute to this industry and the competition is also expected to increase.

High plant quality and low production cost are two main factors that determine success in marketing. Optimum temperature during production is a factor in production cost and plant growth quality. While warmer temperatures can cut cost by shortening the crop time (Seeley, 1985), high temperatures during the warm season in southern states can adversely affect plant quality, since adequate temperature control in production areas is often impossible and unaffordable. Reports of high temperature stress on flower crops have become more common.

In the past decades, considerable effort has been invested into studying heat stress physiology. However, the complex effects of high temperature stress in plant growth require more than one control mechanism and is still not clear. Impatiens have been an important bedding plant since 1982 (Sallee, 1989; Seeley, 1985). They were categorized as a warm temperature crop and were shown to maintain good quality at temperatures of 20 to 32°C (Seeley, 1985). However, they have been reported to be high temperature sensitive (Higuchi et al., 1987; Nelson et al., 1980).

The overall goals of this research were to illustrate the physiological basis for effects of supraoptimal temperature on developing flowers in tolerant and sensitive genotypes of impatiens. The specific objectives of this research are to 1) evaluate genotypes for heat sensitivity; 2)

determine the effects of high-temperature induced water stress on flower development; 3) examine changes in the assimilate partitioning to developing flower buds as affected by supraoptimal temperatures; 4) determine high temperature effects on the activity of invertase, which is believed to be responsible for sucrose breakdown and carbon import in developing buds; and 5) to quantify changes in carbohydrate levels in flower buds. The results of these studies will enhance the understanding the physiology of flower development systems in response to heat stress, and may be applicable to all plant biology.

CHAPTER 2
REVIEW OF THE LITERATURE

Impatiens (*Impatiens wallerana* Hook. f., *I. holstii,I. sultani*) is the only significant bedding plant in the family Balsaminaceae. Today's hybrid impatiens have come from *Impatiens holstii* and *Impatiens sultani* (Carlson and Rowley, 1980). Impatiens are a rather succulent perennials which are native to tropical Africa and Southern Asia. Flowers are fleshy, 5-merous, with a long curved filiform spur, and are usually zygomorphic.

Impatiens, characterized by shade tolerance, colorful flowers, and fast and uniform growth, are not only popular in landscaping and home gardening, but also widely accepted as hanging baskets. Impatiens replaced petunia in 1982 as number one bedding plant in market sales (Sallee, 1989). Impatiens has been categorized as a warm temperature crop that maintains good quality at temperature of 20 to 32°C (Seeley, 1985). However, they have been reported to be sensitive to high temperatures (Higuchi et al., 1987; Nelson et al., 1980).

Temperature

The effect of temperature on crop growth and yield is exceedingly complex as it is usually compounded with other environmental factors, such as light, CO_2 supply, water supply, and nutrients (Levitt, 1980). There is great variability among plants of different species in their ability to adjust metabolic processes to the changes in environment. In addition to genetic control, a number of physiological and biochemical mechanisms have been proposed to be involved in a self-adjustment system of plants in response to external temperature changes.

Normal plant development is dependent on a temperature regime suitable for metabolic activity (Levitt, 1980). Any temperature lower or higher than this regime may cause unfavorable effects on plants and constitute a stress. Nevertheless, it is difficult to give a critical value for a stress temperature because temperature effect is not an independent parameter but a function of plant responses. Hence, different tissues and organs at different developmental stages may respond differently to the same temperature regime (Sutcliffe, 1977).

Some important plant processes have been reported to be affected by supraoptimal yet sub-lethal temperature. These include a reduction in photosynthesis (Caers et al., 1985; Duff and Beard, 1974; Imbamba and Tiezsn, 1977; Nobel and Smith, 1983), alteration of assimilate partitioning (Ho, 1978; Dinar et al., 1983; Dinar and Rudich, 1985a; Morris and Arthur, 1985b; Ruter, 1989; Sepúlveda et al., 1986), changes in water relations (Kramer, 1983; Levitt, 1980), imbalance of endogenous hormones (Abdul and Harris 1978; Hellali and Kester, 1979; Itai et al., 1973), and decrease of enzyme activity (Dinar and Rudich, 1985b; Markus et al., 1981).

Heat Stress

Heat stress has been reported to inhibit shoot and root growth in many crops. Leaves from citrus trees grown in high temperatures (38°/28°C) were smaller but broader than those of controls (Reuther et al., 1979). Young partly expanded leaves became distorted, cupped, and faintly yellow brown in color when exposed to 40°C for 8 days. High temperatures stimulate soft growth, resulting in taller, thin-stemmed plants (Carlson and Rowley, 1980). Within the temperature range of 9 to 36°C, fastest growth was observed at 25°C with a parabolic decrease at lower or higher temperatures (Gent, 1986). Geraniums grown under supraoptimal temperatures (32°C) had thinner leaves and lower leaf specific weight than those in optimal conditions (Abdul and Harris,1978).

High temperature has also been reported to affect flower initiation and development. On tomato plants grown at day temperatures ranging from 18 to 28°C, Sawhney (1983) reported that flower size decreased consistently as temperature increased. Flowers produced in higher temperature also contained smaller numbers of petals, carpels, and locules than did those from lower temperature. Although relatively higher temperatures promoted flower development so as to shorten the time needed to flower (Seeley, 1985), temperatures higher than optimal causes heat delay on many crops. Heat delay, a suspension of flowering caused by high temperature, has long been a common problem on chrysanthemums (Whealy, 1987) and Kalanchoe (Gehrke, 1988) in southern states during warm summer seasons. The typical symptoms of heat delay are delayed floral initiation and differentiation, corolla tube splitting, partial induction of inflorescences, and induced abnormal flowers. The decrease in flower size caused by high temperature stress has been demonstrated on chrysanthemums (Whealy, 1987), geraniums (Armitage et al., 1981) and tomato (El-Abd et al., 1986). The temperature optimum for vegetative growth in chrysanthemums is higher than that for reproductive development, since high temperature exposure (30°/26°C, day/night) promoted leaf and stem growth but had little effect on flower dry weight (Whealy et al., 1987). Tomato plants grown in high temperature were characterized by high flower abscission and poor fruit set (El-Abd et al., 1986).

Water Relationship

Water, in addition to temperature and light, is one of the most important environmental factors in plant development. Almost every plant process is affected directly or indirectly by the water supply. As summarized by Kramer (1983), the importance of water to plants is that water functions as constituent, solvent, reactant, and maintenance of turgidity of plant cells and all related metabolic processes. Therefore, maintenance of adequate water status within a plant is essential for normal growth.

Water potential is a measure of the free energy status of water and is expressed most frequently in units of pressure (Kramer, 1983). Water potential consists of at least three mutually independent components, as shown in the following equation.

$$\Psi_w = \Psi_s + \Psi_p + \Psi_m$$

where Ψ_w is the potential of the water in the cells, and other terms are solute potential (Ψ_s), pressure potential (Ψ_p), and matrix potential (Ψ_m).

Solute potential, a negative value, expresses the decrease in the total water potential due to compounds dissolved in cell solution. Pressure potential is the change in total water potential due to the pressure of cellular water against the cell wall. Pressure potential is usually positive in most plant cells, but negative in the xylem of actively transpiring plants. Matrix potential, also a negative value, is generated by the effects of water-binding colloids and surfaces and the capillary effects in cells and cell walls (Kramer, 1983; Slavik, 1974).

The internal water relations of plants are controlled by the relative rates of water uptake by roots and the water loss through transpiration (Kozlowski, 1968). Transpiration is defined as the loss of water from plants in the form of vapor (Kramer, 1983). This loss of water is mainly through stomata. The rate of transpiration depends on stomatal resistance and on the water vapor gradient between internal evaporating surfaces and bulk ambient air outside the leaves. This gradient is temperature dependent (Gates, 1968; Kaufmann, 1982; Kramer, 1983; Wuenscher and Kozlowski, 1971). Continuous water uptake through roots is necessary for compensating the loss through transpiration to maintain a water balance (Unger et al., 1981). If water loss through transpiration exceeds water uptake, the plants may experience water deficits (Hale and Orcutt, 1987). This stress can result from either excessive transpiration, or decreased water uptake, or the combination of both (Kramer, 1983; Slavik, 1974).

Heat Stress and Water Stress Interrelationship

Heat stress is usually accompanied by water deficit because high temperatures together with low relative humidity favor high rates of transpiration (Lawlor, 1979; Levitt, 1980; Hale & Orcutt, 1987). As pointed out by Levitt (1980), high temperature causes a sharp increase in transpiration because of the increase in the vapor pressure gradient between leaf cells and bulk air. An equivalent to 30 percent drop of atmospheric relative humidity may be expected if the leaf temperature is 5° C above the air temperature (Curtis, 1936). The vapor pressure deficit and the evaporation rates would be twice as great at 30°C as at 20°C although the humidity was 70 percent in both conditions (Kramer, 1983; Slavik, 1974).

Stomatal apertures increase with increasing temperature up to some optimum before closure begins. In a study on high temperature effects on transpiration and diffusive resistance of five different tree species, Wuenscher and Kozlowski (1971) reported that transpiration rates of all five tree species increased as temperature increased from 20°C to 30°C and than decreased as temperature exceeded 30 to 35°C. Nevertheless, the diffusive resistance increased linearly throughout the tested temperature range (Wuenscher and Kozlowski, 1971). Similar results have been obtained on vegetable crops *Amaranthus lividus, Gynandropsis gynandra*, and *Crotalaria brevidens* (Imbamba and Tieszen, 1977) and *Vitis vinifera* (Sepúlveda and Kliewer, 1986b). They attributed the increase of diffusive resistance to either increased internal CO_2 concentration or desiccation of the leaf rather than high temperature alone (Sepúlveda and Kliewer, 1986b; Wuenscher and Kozlowski, 1971). However, opposite results have been reported on *Vicia faba*, where stomata remained open until guard cells were lethally damaged at 45°C and higher (Rogers et al., 1981).

Water Stress and Plant Growth

Plants increase in size mostly because of cell division and cell expansion. The rate of water uptake in intact plants is positively correlated to the gradient of water potential between the source of water and the enlarging cells (Cutler et al., 1980). In general, tissues next to the elongating region have higher water potentials than the developing cells and act as a water source for cell enlargement (Matyssek et al., 1988). With solute accumulation, cells build up osmotic potential and lower the water potential to enhance water uptake from the surroundings. (Nonami and Boyer, 1987; Nonami and Schulze, 1989). However, cell division and cell expansion are the plant processes which are more sensitive to water deficit (Hsiao,1973). Even mild water deficit may affect cell growth.

The fact that water stress decreases cell expansion and leaf elongation has been shown on barley (Matsuda and Raizi, 1981), maize (Michelena and Boyer, 1982; Westgate and Boyer, 1985), soybean (Bunce, 1977; Bunce, 1978; Nonami and Schulze, 1989), and rice (Cutler et al., 1980). Subsequent decreases in leaf and plant size were also observed (Clough and Milthorpe, 1975). Mild water stress at leaf water potentials of -1.1 to -1.4 MPa has been reported to have pronounced inhibition on cell division in sunflower (Yegappan et al., 1980). Leaf primordium formation and leaf unfolding were also slowed by water stress, thus 2.5 fewer unfolded leaves were observed on stressed plants than on controls after a 35 day drying cycle. In another study on sunflower, Takami et al. (1981) pointed out that leaf expansion was reduced markedly as the pre-dawn leaf water potential decreased from -0.35 to -0.6 MPa, and expansion ceased at a pre-dawn leaf water potential of about -1.0 MPa. The duration of leaf expansion was actually increased by stress and the 25-35% reduction in final leaf size was observed on all four tested cultivars. Turgor potential affected expansion even more. With pre-dawn turgor potentials ranging from 0.15 to 0.35 Mpa, a 0.1-MPa decrease in turgor led to a 75% decrease in leaf expansion (Takami et al., 1981).

Plant tissues at different stages may respond differently to water deficit. Work on poinsettia has shown that stress prior to start of long nights had little effect on plant growth, while the inflorescence diameter was significantly reduced if plants were exposed to water deficit after bract coloration (Gilbertz et al., 1984).

Change in area, shape, or orientation of plant leaves has been suggested as means of reducing light interception and transpiration by plants subjected to water stress (Begg, 1980; Kramer, 1983). By rolling the leaves, a decrease of 36 to 47% in transpiration has been observed on *Oryza sativa* (O'Toole and Cruz, 1979). A later report showed that leaf rolling began at relatively high water potential (-8 to -12 bars) and the degree of rolling was linearly related to the decrease of leaf water potential (O'Toole and Crutz, 1980).

Photosynthesis

Photosynthesis is one of the more important processes influenced by temperature. Even though it is a photochemical process, it depends on enzyme activity and CO_2 availability and therefore is temperature dependent (Levitt, 1980). High temperatures which cause a decrease in photosynthetic rate have been reported on both C3 and C4 plants (Bar-Tsur et al., 1985; Berry and Björkman, 1980; Imbamba and Tieszen, 1977; Markus et al., 1981; Moon et al., 1987). About 80 percent inhibition of CO_2 fixation was reported on spinach leaves when temperature was increased from 20°C to 30°C (Weis, 1981). In tomato, an increase in air temperature from 20 to 39°C for 15 hours caused a 75% decrease in photosynthetic rate on a heat sensitive cultivar and a 10% decrease on a heat tolerant one (Markus et al., 1981). Similar results were obtained by Bar-Tsur et al. (1985).

High temperature effects on photosynthesis could be due to stomatal or nonstomatal inhibitions. As temperature increases, decreases in CO_2 assimilation are thought to be attributed

to an increase in mesophyll resistance and decreases in stomatal aperture which, in turn, reduces CO_2 influx (Bar-Tzur et al., 1985; Moon et al., 1987).

Ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBisCo) is an important enzyme in CO_2 fixation. Decline in CO_2 assimilation at high temperature has been reported to be associated with a decrease in carboxylase activity (Laing et al., 1974; Weis, 1981; Kobza and Edwards, 1987). Markus et al. (1981) reported that heat stress (50°C) caused 75 percent reduction in RuBisCo activity in the heat sensitive tomato cultivar Roma VF. In wheat, the ratio of oxygenase/carboxylase increased 2-fold when temperature was increased from 15 to 35°C (Hall and Keys, 1983). It is suggested that the change in oxygenase to carboxylase ratio at high temperature causes the increase of photorespiration, and consequently the decrease of photosynthesis (Jackson and Volk, 1970; Laing et al., 1974; Lawlor, 1979; Moon et al., 1987).

The activity of carboxylase is positively correlated with the CO_2 / O_2 ratio in mesophyll cells. However, this ratio decreases rapidly as temperature increases from 15°C to 30°C (Laing et al., 1974; Lawlor, 1979). It was suggested that the solubility of CO_2 and O_2 in the aqueous surface of mesophyll cells decreased as temperature increased. However, the decrease was greater for CO_2 than for O_2. Consequently, the change in the declining ratio of carboxylase to oxygenase activity may be expected to cause changes in the ratio of photosynthesis to photorespiration.

Electron transport reactions associated with thylakoid membranes in PS I and PS II are more sensitive to high temperature than are soluble enzymes in chloroplasts (Chetti and Nobel, 1987; Goltsev et al., 1987; Santarius, 1975). The decline in the rate of electron transport reactions at stress temperatures could be due to heat-induced damage to electron transport components as well as direct damage to the pigment systems (Armond et al., 1978). High temperature stress may damage the membrane integrity of the photosynthetic apparatus (Goltsev et al., 1987). Venediktov and Krivoshejeva (1984) reported that heat denaturation of membrane proteins was the most probable mechanism for inactivation of chloroplast.

Net photosynthesis decreases when plants are subjected to water stress. Mild water stress (-1.0 to -1.5 MPa) has been shown to reduce photosynthetic rates significantly in soybean (Bunce, 1982; Huber et al., 1984), sunflower (Bunce, 1982), and cacao (Deng et al., 1990). In peanut, large reductions in photosynthesis and stomatal conductance were observed when leaf relative water content (RWC) decreased from 80 to 75% (Bhagsari et al., 1976). Leaf water potential appeared to be the best indicator of a rapid decrease of photosynthesis in geranium (Armitage and Vines, 1983). As leaf water potential dropped from -2 to -14 bars, photosynthetic rate decreased from maximum to slow decline, to rapid decline, to total inhibition. The highest photosynthesis was observed when RWC was 91% and higher, and it dropped sharply when RWC was lower than 84%. It was suggested that water stress acts in the same way as heat stress, by affecting photosynthesis through stomatal closure and increased mesophyll resistance (Bunce, 1982; Huber et al., 1984; Vassey and Sharkey, 1989).

Carbohydrate and Flower Development

Carbohydrate level is an important factor for flower initiation and development (Halevy, 1987; Mor and Halevy, 1979). It is generally agreed that developing buds act as major sinks which intensively use carbohydrates and other metabolites under favorable growing conditions (Halevy, 1987; Mor and Halevy, 1979; Russell and Morris, 1983). At an early stage in flower development the absolute percentage of ^{14}C assimilates translocated to the flower buds is small, but their relative specific activity, representing the relative sink activity, is very high (Mor and Halevy, 1979). During flower development, continuous accumulation of dry matter and water is necessary for the expansion and elongation of epidermal cells and consequent petal enlargement and flower opening (Koning, 1984). In rose, accumulation of reducing sugars and starch has been reported to continue throughout most of the corolla development (Ho and Nichols, 1977). However, when plants were under stress that limited the supply of essential assimilates, the young

flower buds became a weak sink in comparison with the vegetative sink and competed poorly for the available assimilates (Halevy, 1987; Hariss and Jeffcoat, 1974; Ho, 1984; Russell and Morris, 1982). Elphinstone et al. (1986) reported that high temperature together with long photoperiod caused the abortion of iris flower buds, because of the promotion of vegetative sink activity and more metabolite partitioning to daughter bulbs. Any treatment that can enhance carbohydrate level may promote flower development. Work on tomatoes showed that the removal of developing leaves (competing sinks) at the shoot apex leads to a promotion of flowering (Kinet, 1977) and to a substantial increase in the rate of inflorescence growth (Russell and Morris, 1982).

There is evidence that the effect of temperature on flower development may involve photosynthate production, translocation, and/or accumulation. High temperature was reported to cause a reduction in flower and fruit size (Whealy, 1987; Armitage et al., 1981; Matusi et al., 1986; Satti and Oebker, 1986). High field temperatures of 32 to 42°C caused a 30 to 35% reduction in both starch and soluble sugar content in tomato flowers (Satti and Obeker, 1986). The authors postulated that the lower carbohydrate content resulted in much reduced flower size (Satti and Obeker, 1986). In carnations grown at 6 to 18°C, flower buds presented as strong sinks even at highest temperature (Harris and Scott, 1969). However, the absolute dry weight and final size of flowers grown in high temperature were reduced because high temperature enhanced the rate of flower development and shortened the filling period.

Assimilate Partitioning

Plant growth and yield involve the integration of photosynthetic carbon assimilation in source leaves and its subsequent allocation to and utilization by sink tissues. Carbon exported from leaves may be distributed to new shoots, roots, and reproductive tissues. The amount of assimilate uptake by sink tissue depends on the ability of this tissue to compete for the available

assimilate with other sinks. This ability is termed as 'sink strength' which is a function of sink size and sink activity.

Assimilate partitioning between sink and source is dynamic (Walker and Ho, 1977), and is regulated by the interaction between sink demand and assimilation (Ho, 1977; Zeevaart, 1979). Primarily, sink demand is determined by both growth and respiration in the sink organs (Ho, 1979). However, the mechanisms controlling partitioning of assimilates between competing sinks are not fully understood. There is increasing evidence to suggest that rate of import of carbohydrates by sink organs is not determined by the rate of concurrent assimilation but by the rate of assimilate utilization (Ho, 1979; Walker and Ho, 1977; Wardlaw, 1974). This view is supported by the observation that the partitioning of newly fixed carbon to starch was positively proportional to the rate of photosynthesis, while the rate of carbon export was only slightly affected by changes in photosynthetic rate (Grange, 1985).

Sucrose is a major form of transport carbon in most plant species. The transport of sucrose from source leaves to various metabolic sink organs is composed of a series of components. Sucrose is transported through cytoplasmic connections between photosynthetic cells until it reaches phloem, then moves into the apoplast or free space by a process of facilitated diffusion. It is then actively loaded into phloem cells by a metabolically-driven process which results in a very high sucrose concentration in sieve tubes (Beevers, 1985). The low osmotic potential at the source end causes water influx which drives mass-flow (Geiger, 1976). Movement of solutes in phloem depends on the turgor pressure gradient between the source and sink. The maintenance of this pressure gradient depends on continuous loading of sucrose into the source end of the transport path, and its removal at the sink end by either metabolism or by storage compartmentation (Wareing and Patrick, 1975). Once sucrose arrives at sink tissues, it may be transported into the sink cells via symplastic route through plasmodesmata, or it can be unloaded into the apoplast prior to uptake by sink cells (Giaquinta et al., 1983; Gifford et al., 1984; Stanzel et al., 1988). According to the sink classification by Ho and Baker (1982), most actively

growing tissues, i.e. young leaves and meristems, import sugars via symplast, and the rate of import is mainly controlled by the metabolic activity within the sinks. There is evidence that a continuous symplastic connection exists between sieve elements and surrounding tissues in young leaves (Giaquinta, 1977).

High temperature affects assimilate partitioning. Export of radioactive assimilates from source leaves was inhibited in high temperature regimes (Dinar et al., 1983). Assimilate transport to tomato flower buds was inhibited by heat stress conditions (38/25°C, day/night) more in a heat sensitive cultivar 'Roma VF' than in heat tolerant 'Saladette' (Dinar and Rudich, 1985a; 1985b). It is possible that the process of assimilate transport from leaves to the flower buds was limited either by the supply from the source or by the mobilizing ability of the sink organs. Heat stress has been previously reported to reduce carbon fixation by plant leaves (Bar-Tsur et al., 1985; Markus et al., 1981). A positive correlation between carbon fixation and its export was observed in tomato leaves (Ho, 1978). Hence, the significant reduction in carbon fixation in response to heat stress may result in a reduction of the total carbon pool within the leaf, thereby limiting total carbon transport from the source leaves (Dinar et al., 1983). A similar study has been conducted on grapevine cultivar 'Chardonnay'. Sepúlveda et al. (1986) demonstrated that, under heat stress (40/20°), assimilate was predominantly partitioned toward the shoot tip. They concluded that heat stress caused changes in the distribution patterns of photosynthate in grapevine and that these changes are related to the shift of growth responses of the different sinks throughout the plant. Callose formed in sieve plates of plants subjected to heat stress may also decrease carbon transport (McNairn, 1972).

When pearl millet was grown under temperatures higher than optimal, the total yield decreased due a decrease in the time for panicle filling (Squire, 1989). Shishido et al. (1987) reported that elevated air temperature from 25 to 30°C stimulated allocation of assimilate to root growth at the expense of young leaves. Altering either the demand for photosynthate by grain removal, or the supply of photosynthate by defoliation and shading treatment, did not prevent the

reduction in grain yield due to high temperature (Nicolas et al., 1984; Wardlaw et al., 1980). The results indicated that the temperature effect occurred mainly within the grain itself and was not from an effect on the availability of photosynthate. This concept agreed with the study on the uptake of ^{14}C-sucrose by detached tomato flower buds where the inability of young heat-stressed flower buds to take up sucrose was due to their low sink strength (Dinar et al., 1983).

Invertase and Sucrose Metabolism

Beta-Fructofuranosidase (EC 3,2,1,26) catalyzes the reaction shown below and specifically hydrolyses the bond between C(2)-O on the fructose moiety of sucrose (Whitaker, 1972). (The numbers under the compounds represent the specific rotations).

$$\underset{-66.5^{\circ}}{\text{Sucrose}} + H_2O \text{ ------->} \underset{+52.2^{\circ}}{\text{Glucose}} + \underset{-93^{\circ}}{\text{Fructose}}$$

Because of the inversion of rotation ($+66.5^{\circ}$ to -20.5°) of the solution during reaction, the enzyme became known as invertase.

Invertase is found in plant tissues in several forms differing in pH optima and cellular localization. The acid invertase has a pH maxima of 4.5-5.5 and apparent Km of 2.5-3.3 mM sucrose (Hawker et al., 1976; Masuda et al., 1988; Woodson and Wang, 1987), while the alkaline invertase (or neutral) has pH maxima of 6.8-7.5 and apparent Km of 20-30 mM sucrose (Schaffer, 1986). There is a transition of invertase activity as plant tissues develop. Acid invertase is predominant in young, enlarging tissues, while alkaline invertase is predominant in mature tissues (Claussen et al., 1985; Morris and Arthur, 1984a; 1984b; Ricardo and Ap Rees, 1970). Soluble invertase is found wildly distributed while cell-wall bond invertase is found primary in storage tissues (Stanzel et al., 1988; Lowell et al., 1989). Young flower buds and leaves usually have a high activity level of soluble acid invertase, while the activities of alkaline and cell-wall bond

invertase are low or undetectable (Morris and Arthur, 1984a; Pollock and Lloyd, 1977; Woodson and Wang, 1987; Hawker et al., 1976). Although sucrose synthase degrades sucrose also, its activity in flower tissues is usually much less than that of acid invertase (Hawker et al., 1976; Woodson and Wang, 1987).

That high temperatures modify sucrose breakdown and sugar metabolism in sink tissues was considered a main factor affecting assimilate distribution (Ho, 1979; Dinar and Rudich, 1985b). In studies of heat stress effects on carbon metabolism in young fruit and flower buds of tomato plants, a negative correlation between sucrose accumulation and uptake in the tissues was found by Dinar and Rudich (1985a and 1985b). They suggested that the rate of carbon transport in plants may be controlled by the gradient of sucrose concentration between sources and sinks. Sucrose levels and starch content in flower buds were found to be closely related because most of the carbon accumulated in buds results from the import of sucrose and was present in the form of starch and insoluble residues (Dinar and Rudich, 1985b).

In normal conditions, growth rate and assimilate import by a sink organ are usually related. It is suggested that heat stress might limit both organ growth rate and carbon import in young flower buds by modifying sucrose metabolism. The accumulation of sucrose in the flower bud may inhibit further sucrose import and restrict the supply of available glucose necessary for processes requiring energy (Dinar and Rudich, 1985a, 1985b). Although a high level of sucrose was observed in both leaves (source) and flower buds (sink), the pool of hexose and starch was decreased (Gent, 1986; Satti and Obeker, 1986). Accumulation of sucrose in leaves was probably due to a reduction in assimilate transport (Dinar et al., 1983), however, inhibition of sucrose hydrolysis in young flower buds cannot be ruled out as a response to heat stress (Dinar and Rudich, 1985b; Walker and Ho, 1977).

Environmental stresses have been reported to inhibit invertase activity in developing tissues. Salt stress was shown to lead to correlated decreases in the rate of leaf expansion and invertase activity in *Phaseolus vulgaris* L. and *Zea mays* L. (Hawker and Walker, 1978). Decrease

in activity of the enzyme invertase in flower buds was reported to be responsible for the sucrose accumulation that resulted from heat stress (Gent, 1986; Rusell and Morris, 1982). In source-leaf removal experiments in tomato, the reduced inflorescence growth rate and flower bud development index were consistently associated with low reducing sugar concentrations, low reducing sugar/sucrose ratios and low invertase activities. Conversely, removal of young leaves at the shoot apex stimulates dry matter accumulation by the inflorescence and increases its acid invertase activity (Ho, 1979). Walker and Thornley (1977) suggested that the rate of carbon import and inflorescence development in the tomato may be controlled by an invertase-mediated mechanism which ensured that the rate of sucrose import could be precisely matched to the rate of its utilization. Under high temperature conditions, a higher invertase activity was observed in the heat tolerant cultivar 'Saladette' than the heat sensitive 'Roma VF' tomato (Bar-Tsur et al., 1985).

Alternatively, the regulation of invertase synthesis in the developing inflorescence may be under hormonal control by the flower buds. In a range of species, increases in cell growth rate and/or assimilate import induced by IAA, gibberellin or cytokinin applications have been found to be closely correlated with increases in acid invertase activity (Morris, 1982; Ho, 1984; Morris and Arthur, 1985b). A study on sucrose transport and metabolism in sugar cane has provided evidence to indicate that the synthesis of invertase in the stem storage tissues was promoted by auxin application (Ryle and Powell, 1972).

CHAPTER 3
HIGH TEMPERATURE EFFECTS ON THE GROWTH AND FLOWERING OF *IMPATIENS WALLERANA* CULTIVARS

Introduction

The effects of temperature on growth and development have been evaluated in many plant species. Warmer temperatures enhance plant growth and flower opening, hence, reducing bedding plant production costs by shortening greenhouse occupation time (Seeley, 1985). However, in warm climates, high temperature can persist throughout the production period and adversely affect plant quality. As shown by Armitage et al. (1981) and Sawhney (1983), temperatures higher than optimal could increase respiration rates, decrease net photosynthesis and dry matter production, and decrease flower size.

Impatiens are important bedding plants in many areas (Sallee, 1989). They are shade tolerant in the landscape, yet flowering is better in full sun conditions (Kerstjens, 1980). Nevertheless, impatiens have been reported to be more sensitive to high temperature than many other bedding plants (Higuchi et al., 1987). Since significant temperature control during the production period is often impossible or unaffordable and different genotypes may respond differently to the same temperature regime as observed in chrysanthemum (Whealy et al., 1987) and tomato (El Ahamadi and Stevens, 1979), careful cultivar selection could partly offset the adverse effects of high temperature. The objectives of this experiment were to evaluate the temperature effects on growth and flowering of impatiens and to identify cultivars that are less sensitive to high temperature.

Material and Methods

Nineteen cultivars of *Impatiens wallerana* (Table 3-1) were used in this experiment. On 14 January 1988, uniform seedlings were obtained as plugs from a commercial grower (Natural Beauty of Florida, Apopka, Florida) and planted in 10-cm pots in Vergro Klay Mix. Plants were grown in a greenhouse under natural daylength at 27.5 ± 2.5°C maximum day and 17.5 ± 2.5°C minimum night temperatures for 3 weeks. Then, plants were separated into three 5 m x 6 m greenhouses with day/night temperature regimes of 34/29 (high), 29/24 (intermediate), or 24/18°C (low) for 4 weeks starting 5 February 1988. Temperature fluctuation was 2°C above or below the set temperature. Average midday light level was 800 μmol m^{-2} sec^{-1} and relative humidity ranged from 50 to 70%. Plants were watered as needed to prevent wilting. The experiment was a split-plot design with four replicates and two plants in each experimental unit.

Plant size, flower diameter, flower number per plant, and shoot dry weight were determined at the end of the experiment. Plant size was computed based on the sum of height and width values divided by two. Flower diameter was the average of two widths measured vertically. At the end of experiments, all above ground tissues were harvested, oven dried at 70°C for 72 hrs, then weighed for shoot dry weight. Shape and flower quality of each plant was rated by four individuals at the termination of the experiment. The rating system ranged from 1 to 5 where: 1=poor, 2=fair, 3=average, 4=good, and 5=excellent. Flower quality was visually rated according to the coloration and number of flowers and the extent of petal opening. Whole plant quality was determined by summing the visual grade of plant shape and flower quality. A whole plant visual grade of 6 or greater is considered acceptable for landscape use in the treated temperature regime.

Results and Discussion

Plant size tended to increase as temperature was increased from 24/18 to 34/29°C (Table 3-1). Longer internodes were observed on plants of all cultivars grown in higher temperatures, which resulted in less compact plant shape as compared with plants grown in lower temperature regimes. There were differences in cultivar responses to increasing temperature. The cultivars 'Blitz Violet' and 'Show Stopper Lt. Lavender' increased by more than 30% between the lowest and highest temperature, but 'Super Elfin Red Velvet' increased by only 15%. Shoot dry weight generally increased with increasing temperature, also (Table 3-2). However, the amount of increase was not as great as for plant size, and the differences among cultivars at any one temperature varied more than with size. 'Show Stopper Lt. Lavender', 'Super Elfin Pink', and 'Super Elfin Twilight' had the greatest increase with temperature, while 'Dazzler Pink' had a slight decrease with increasing temperature.

All plants grown under the high (34/29°C) temperature regime had smaller flowers compared to those grown under the low (24/18°C) temperature regime (Table 3-3). The effect of the increase from 24/18 to 29/24°C was greater than from 29/24 to 34/29°C. 'Blitz Violet' had the largest flowers at each temperature, but its response to temperature was about average. 'Super Elfin Salmon' flower size decreased by 33% from 24/18 to 34/29°C, but 'Accent Violet' decreased by only 13%. Most cultivars had fewer flowers in 24/18°C compared to 29/24 and 34/29°C (Table 3-4). This was due to slower bud development and opening at 24/18°C, especially on cultivars 'Blitz Violet', 'Show Stopper Lt. Lavender', 'Super Elfin Red', and 'Super Elfin Salmon'.

It has been shown that within a plant's optimal temperature range, increasing temperatures enhance vegetative growth (Whealy et al., 1987; Seeley, 1985; De Jong and Smeets, 1982). Our results indicate that both vegetative growth and flowering of Impatiens are affected by air temperature. Apparently, high (34/29°C) temperature stimulates vegetative growth as

Table 3-1. Final plant size for 19 impatiens cultivars after being held at day/night temperatures of 34/29, 29/24, or 24/18°C for 4 weeks.

Cultivar	Final plant size[z] (cm)		
	34/29°C	29/24°C	24/18°C
Accent Pink	25.3	23.5	19.6
Accent Red	26.6	23.2	20.3
Accent Rose	27.4	26.2	22.0
Accent Salmon	28.9	24.1	22.8
Accent Violet	28.7	25.2	22.4
Blitz Violet	31.8	27.1	23.4
Dazzler Orange	28.2	22.9	21.2
Dazzler Pink	25.8	24.5	20.4
Dazzler Red	26.6	25.7	21.5
Dazzler White	27.0	24.4	21.1
Show Stopper Lt. Lavender	33.4	29.3	25.0
Super Elfin Bright Eye	29.6	26.3	24.3
Super Elfin Orange	28.1	25.0	23.6
Super Elfin Pink	29.4	25.0	22.7
Super Elfin Red	28.0	24.6	22.5
Super Elfin Red Velvet	27.7	24.2	24.5
Super Elfin Rose	30.0	25.3	22.9
Super Elfin Salmon	28.0	25.4	22.4
Super Elfin Twilight	29.4	25.4	22.1
Temperature		.0001	
Cultivar		.0001	
Temperature x Cultivar		.0001	

[z] Size= the sum of height and width values divided by 2.

Table 3-2. Total shoot dry weight for 19 impatiens cultivars after being held at day/night temperatures of 34/29, 29/24, or 24/18°C for 4 weeks.

Cultivar	Shoot dry weight[z](g)		
	34/29°C	29/24°C	24/18°C
Accent Pink	4.74	4.35	4.03
Accent Red	4.42	4.32	3.95
Accent Rose	5.01	5.01	4.47
Accent Salmon	5.56	4.07	4.80
Accent Violet	4.49	3.88	4.02
Blitz Violet	6.35	5.75	5.56
Dazzler Orange	4.57	4.08	3.84
Dazzler Pink	4.67	4.71	4.82
Dazzler Red	4.83	4.74	4.39
Dazzler White	5.48	4.77	4.90
Show Stopper Lt. Lavender	6.93	6.19	5.73
Super Elfin Bright Eye	5.88	5.31	5.62
Super Elfin Orange	5.46	4.80	4.91
Super Elfin Pink	6.28	5.24	4.58
Super Elfin Red	5.92	5.15	5.48
Super Elfin Red Velvet	5.23	4.46	5.10
Super Elfin Rose	5.39	4.67	4.59
Super Elfin Salmon	5.73	5.82	5.25
Super Elfin Twilight	6.23	5.61	5.29
Temperature		.0001	
Cultivar		.0001	
Temperature x Cultivar		.0006	

[z] All above-ground parts including leaves and flowers.

Table 3-3. Changes in flower diameter for 19 impatiens cultivars after being held at day/night temperatures of 34/29, 29/24, or 24/18°C for 4 weeks.

Cultivar	Flower size[z](cm)		
	34/29°C	29/24°C	24/18°C
Accent Pink	3.8	4.1	5.0
Accent Red	3.8	3.9	5.1
Accent Rose	4.0	3.9	4.9
Accent Salmon	3.7	3.9	5.2
Accent Violet	4.6	4.4	5.3
Blitz Violet	4.9	4.9	6.0
Dazzler Orange	4.0	4.3	5.0
Dazzler Pink	4.2	4.2	5.3
Dazzler Red	3.7	4.2	5.2
Dazzler White	4.1	4.4	5.2
Show Stopper Lt. Lavender	4.6	4.4	5.7
Super Elfin Bright Eye	3.9	3.7	4.5
Super Elfin Orange	4.1	4.2	5.4
Super Elfin Pink	4.1	4.3	4.9
Super Elfin Red	3.9	4.2	5.1
Super Elfin Red Velvet	3.9	4.1	5.2
Super Elfin Rose	3.8	3.8	5.2
Super Elfin Salmon	3.3	3.7	4.9
Super Elfin Twilight	3.9	3.9	5.2
Temperature		.0001	
Cultivar		.0001	
Temperature x Cultivar		.0001	

[z] Average of 2 diameters measured vertically.

Table 3-4. Average flower numbers per plant for 19 impatiens cultivars after being held at day/night temperatures of 34/29, 29/24, or 24/18°C for 4 weeks.

Cultivar	Flower number		
	34/29°C	29/24°C	24/18°C
Accent Pink	50	48	24
Accent Red	34	28	25
Accent Rose	46	41	27
Accent Salmon	49	45	28
Accent Violet	35	36	30
Blitz Violet	16	20	9
Dazzler Orange	31	32	26
Dazzler Pink	54	51	31
Dazzler Red	24	29	17
Dazzler White	46	43	31
Show Stopper Lt. Lavender	23	27	7
Super Elfin Bright Eye	34	42	30
Super Elfin Orange	31	32	26
Super Elfin Pink	41	40	25
Super Elfin Red	25	29	9
Super Elfin Red Velvet	28	28	32
Super Elfin Rose	40	40	25
Super Elfin Salmon	13	20	5
Super Elfin Twilight	24	30	11
Temperature		.0001	
Cultivar		.0001	
Temperature x Cultivar		.0001	

shown by increased plant canopy size and shoot dry weight. Similar results have been observed on geraniums (White and Warrington, 1988;) and chrysanthemum (Whealy et al., 1987).

Higher (34/29 and 29/24°C) temperature increases the rate of flower bud development, hence increased flower number on impatiens. It has been shown on geraniums that the number of days needed from visible bud to flower decreased as air temperature increased from 15 to 32°C (Armitage et al., 1981). Therefore, the longer period required for bud development may account for fewer flowers on the plants grown under 24/18°C. High temperature was also reported to decrease flower size of tomato (El-Abd et al., 1986; Sawhney, 1983) and geranium (Armitage et al., 1981) when temperature was increased from 18 to 28°C and from 15 to 32°C, respectively. But the authors did not monitor plant dry weights to relate them to flower size changes. In chrysanthemum, high temperature (30/26°C) increased leaf and stem dry weight but had little effect on final inflorescence dry weight (Whealy et al., 1987). Interestingly, we found that flower diameters of most cultivars grown at high temperature decreased while shoot dry weights increased. Possibly, the decrease of flower size was not due to a shortage of photosynthate at the whole plant level. Assimilate partitioned to the flower buds of tomato plants has been shown to be inhibited by high temperature (Dinar et al., 1983; Dinar and Rudich, 1985a). Further evidence indicates that removal of young leaves will stimilate assimilate accumulation in and development of inflorescences (Ho, 1979; Kinet, 1977). Since phytohormones are involved in flower development (Halevy, 1987; Whealy et al., 1987; Sawhney, 1983), and water potential is of importance in cell growth and expansion (Hsiao, 1973; Taiz, 1984), hormonal imbalance and/or water potential changes during high temperature treatment may be possible contributing factors.

Plants grown at 24/18°C generally were more compact and had darker green leaves. The changes in plant quality and flower ratings due to temperature varied with cultivars. Low quality ratings at 34/29°C were due to excessive stem elongation for all cultivars, curling of leaves and cupped flower in 'Accent Salmon', 'Dazzler Pink', 'Dazzler Red', 'Super Elfin Bright Eye', 'Super Elfin Red', 'Super Elfin Red Velvet', and 'Super Elfin Salmon'. At low temperature, 'Show Stopper

Lt. Lavender', 'Super Elfin Red', 'Super Elfin Salmon', and 'Super Elfin Twilight' were rated low for flower quality because of having so few flowers.

Different cultivars demonstrated distinct growth patterns in the three temperature regimes. Some cultivars had lower quality because of curling leaves and cupped flowers in the high temperature regime, while other cultivars were lower quality due to fewer flowers on plants in the low temperature regime. Most cultivars in the low temperature regime had better quality of plant shape because of compactness.

Based on the quality ratings (Table 3-5) and using a sum of 6 for a minimum acceptable level, 'Show Stopper Lt. Lavender' and 'Super Elfin Salmon' did not perform adequately at any temperature regime. 'Blitz Violet', 'Dazzler Red', 'Super Elfin Red Velvet', and 'Super Elfin Twilight' were satisfactory at only the low temperature. Only three cultivars, 'Accent Pink', 'Dazzler Pink', and 'Dazzler White' were rated adequate at the high temperature. During warm production season, careful selection of cultivars is recommended.

Table 3-5. Visual rating of flower quality and plant shape for 19 impatiens cultivars after being held at day/night temperatures of 34/29, 29/24, or 24/18°C for 4 weeks.

Cultivar	Flower quality[z]			Plant shape[z]		
	34/29°C	29/24°C	24/18°C	34/29°C	29/24°C	24/18°C
Accent Pink	3.5	4.0	3.4	3.3	4.1	4.5
Accent Red	2.8	3.2	3.8	2.6	3.7	4.2
Accent Rose	3.1	3.6	3.8	2.7	3.3	4.0
Accent Salmon	3.5	3.9	3.3	2.5	3.8	3.8
Accent Violet	2.7	3.3	3.7	1.4	3.0	3.7
Blitz Violet	2.0	2.6	2.8	1.1	2.1	3.3
Dazzler Orange	2.7	3.3	3.6	2.2	3.2	3.7
Dazzler Pink	4.2	3.6	4.0	3.4	3.7	4.5
Dazzler Red	2.2	2.7	2.7	2.3	2.6	3.9
Dazzler White	4.4	3.9	3.5	2.9	3.8	4.0
Show Stopper Lt. Lavender	2.3	2.8	1.9	1.1	2.4	3.2
Super Elfin Bright Eye	2.1	3.4	3.6	1.8	2.8	3.5
Super Elfin Orange	2.8	3.1	3.4	2.6	3.3	3.4
Super Elfin Pink	3.5	4.0	3.5	2.4	3.2	3.9
Super Elfin Red	2.4	2.8	1.8	2.9	3.9	4.2
Super Elfin Red Velvet	2.4	2.8	3.4	2.1	2.9	3.3
Super Elfin Rose	2.7	3.3	3.3	1.8	3.5	3.7
Super Elfin Salmon	1.3	1.9	1.3	3.1	3.5	4.3
Super Elfin Twilight	2.3	2.6	1.8	2.3	3.4	4.3
Temperature		.0383			.0001	
Cultivar		.0001			.0001	
Temperature x Cultivar		.0001			.0001	

[z] Average of four individual values with 1=poor, 2=fair, 3=average, 4=good, 5=excellent.

CHAPTER 4
DIFFERENTIAL EFFECTS OF HIGH TEMPERATURE ON TWO IMPATIENS CULTIVARS

Introduction

Temperature effects on flower development have been studied intensively for decades. Several papers have described the adverse effects of high temperatures on flower initiation and development (Amitage et al., 1981; El-Abd et al., 1986; Gehrke, 1988; Harris and Jeffcoat, 1974; Kinet et al., 1985; Whealy, 1987). Some reports have observed smaller flowers in higher temperatures compared to lower temperatures (Armitage, 1981; El-Abd et al., 1986; Gehrke, 1988; Sawhney, 1983; Whealy, 1987); however, the basis for the smaller flower sizes has not been established (Dinar et al., 1983; Harris and Scott, 1969; Satti and Oebker, 1986; Whealy, 1987).

Among the many environmental factors, temperature has profound effect on photosynthesis (Levitt, 1980). Air and/or root temperatures have been demonstrated to inhibit plant photosynthesis at temperatures higher than optimal, and the inhibition could be due to stomatal and/or nonstomatal factors (Johnson and Ingram, 1984; Moon et al., 1987; Ruter, 1989; Tenhunen et al., 1984; Weis, 1981). Photosynthesis in different species or cultivars respond differently to high temperature, and this may reflect the different tolerance and adaptability to heat stress (Bar-Tsur et al., 1985; Björkman et al., 1980; Markus et al., 1981).

In preliminary experiments, we found that impatiens flower development and vegetative growth were affected by high temperature (34/29°C, day/night). Most cultivars performed satisfactory in cool to warm temperatures and seemed to be sensitive to temperatures above 34/29°C. Nevertheless, there existed some cultivar differences. 'Dazzler White' was found to

maintain good plant quality at 34/29°C. Flower bud opening was reduced in 'Super Elfin Red Velvet', although the initiation of flower buds was apparently not affected. These two cultivars were selected as heat resistent and heat sensitive cultivars for this study. The objectives of this study were to further identify the heat sensitivity of these two cultivars and to clarify whether the decrease in flower sizes was the result of high-temperature inhibition on photosynthesis.

Materials and Methods

Uniform seedlings of 'Dazzler White' and 'Super Elfin Red Velvet' were obtained as plugs from Natural Beauty of Florida in Apopka, Florida. The cultural practices were the same as in Experiment 1 of Chapter 3.

Experiment 1. After being grown in a greenhouse at 32 $\pm$ 2.5°C maximum day temperature and 20 $\pm$ 2.5°C minimum night temperature for 3 weeks, plants were moved to three 5 m x 6 m greenhouses at day/night temperature regimes of 39/31, 33/26, or 28/20°C starting 10 July 1988. Temperature fluctuation was 2°C above or below the set temperature. Average midday light level was 800 μmol m^{-2} sec^{-1} and relative humidity was 50 to 70%.

Flower size was determined after 1, 2, 4, and 8 days by averaging two vertical diameters on one flower per plant. Only the flowers opening on those specific days were measured. The experiment was in a split-plot design with four replicates and two plants per experimental unit.

Experiment 2. Plants grown for 3 weeks in standard conditions were moved into greenhouses at day/night temperature regimes of 38/30 or 28/20°C on 17 March 1989. Plant size was recorded at the beginning of and 2 weeks after the start of treatment. Plant size was determined as previously described in Chapter 3. Photosynthesis rates and stomatal conductances were measured at midday on day 14 in the treatments using a portable photosynthesis system (LI-COR model 6200, LI-COR Inc., Lincoln, NE 68504). The most recently

expanded leaf was sampled for each plant. The experiment was in a completely random design with six plants per treatment.

Results and Discussion

Experiment 1. Flower size was smaller for both cultivars under higher day/night temperatures (Table 4-1). This is in agreement with preliminary experiments and with previous results on geraniums (Armitage et al., 1981), tomato (El-Abd et al., 1986), and chrysanthemums (Whealy, 1987). Flower size decreased with increased time at higher temperature. However, the change in flower sizes exhibited an interaction between temperature and duration in temperature treatment. After 8 days, flower size on plants at 33/25°C decreased 11% (0.43 cm) while those at 38/30°C showed a 20% (0.83 cm) decrease. The flower size for plants in 28/20°C changed little over the duration of the experimental period.

High temperatures hasten flower development and shorten the duration from young bud stage to flower opening in carnation, consequently, flower dry weight and flower size at higher temperatures were reduced (Harris and Scott, 1969). Some authors have postulated that assimilate partitioning (Dinar et al., 1985a; 1985b; Halevy, 1987), carbohydrate metabolism (Dinar et al., 1983), and/or endogenous hormone levels (Morris and Arthur, 1985b), in the flower tissues may be altered by high temperatures and directly or indirectly affect flower development and size. However, these processes do not seem to be capable of having dramatic direct effects that would cause a significant decrease in flower sizes within only one to two days after high temperature treatment as observed in this study. Water stress, which has been reported to cause daily shrinkage in sizes of citrus and cherry fruits, may be responsible for the rapid response to high temperatures (Chaney and Kozlowski, 1971; Kozlowski, 1968).

Experiment 2 High temperature (38/30°C) inhibited the growth of both 'Dazzler White' and 'S.E. Red Velvet' (Table 4-2). Final plant size for plants in higher temperature was about 25%

Table 4-1. Flower size for impatiens cultivars 'Dazzler White' and 'S.E. Red Velvet' after being held at day/night temperatures of 39/31, 33/26, or 28/20°C for 1, 2, 4, or 8 days.

Temperature treatment (°C) (day/night)	Cultivar	Flower size[z] (cm)			
		Day 1	Day 2	Day 4	Day 8
39/31	Dazzler White	4.0	3.8	3.6	3.5
33/26	Dazzler White	4.2	4.0	3.8	3.8
28/20	Dazzler White	4.4	4.4	4.5	4.3
39/31	S.E. Red Velvet	4.0	3.7	3.3	2.9
33/26	S.E. Red Velvet	4.1	3.8	3.6	3.7
28/20	S.E. Red Velvet	4.3	4.4	4.4	4.2

Temperature	.0001
Cultivar	.0001
Day	.0001
Temperature x cultivar	.0076
Temperature x day	.0001
Cultivar x day	.0796
Temperature x cultivar x day	.0001

[z] Only flowers opened on those specific days were measured.

Table 4-2. Final plant size and increase in size for impatiens cultivars 'Dazzler White' and 'S. E. Red Velvet' after being held at temperature regimes of 38/30 or 28/20°C for 2 weeks.

Temperature treatment (°C) (day/night)	Final plant size[z] (cm)		Increase in size (cm)	
	Dazzler White	S.E. Red Velvet	Dazzler White	S.E. Red Velvet
38/30	12.2	12.4	2.9	2.4
28/20	15.7	17.1	6.6	7.3
Temperature	.0001		.0001	
Cultivar	.1850		.2019	
Temperature x cultivar	.0451		.0003	

[z] Size= the sum of height and width values divided by 2.

smaller than those in lower temperature. Increase in plant size was 2.3 (Dazzle White) and 3.1 (S.E. Red Velvet) times greater on plants in lower temperature than in higher temperature. Either the final plant size or the increase in size exhibited cultivar-temperature interactions, but cultivar effect was not significant.

High temperature inhibited photosynthesis but there were differences between the two cultivars (Table 4-3). There was more than a 50% decrease in photosynthesis for 'S.E. Red Velvet' plants in high temperature compared to the low temperature treatment. The difference in photosynthesis rate for 'Dazzler White' in the two temperature treatments was only 21%. Similar results have been shown on tomato, where heat stress reduced photosynthesis more in the heat-sensitive cultivar 'Roma' than in the heat-tolerant 'Saladette' (Bar-Tsur et al., 1985; Markus et al., 1981).

High temperatures had little effect on stomatal aperture as the water vapor conductance did not show much difference for either cultivar in the two temperature regimes (Table 4-3). Open stomata together with high temperature could result in high transpiration rates, which would fit into the general concept that heat stress is often accompanied by water stress resulting from excessive transpiration (Hsiao, 1973; Kramer, 1983; Levitt, 1980). In these two experiments, some plants in the highest temperature treatment showed wilt symptoms during midday and early afternoon. This would be another reason to suspect that the quick change in flower sizes were mainly due to water stress, since cell expansion is the plant process most sensitive to water stress (Hsiao, 1973)..

Temperatures higher than optimal have been reported to have both stomatal and nonstomatal effects on photosynthesis (Bar-Tsur et al., 1985; Kobza and Edwards, 1987). As temperature increased, decreased photosynthesis was sometimes thought to be associated with the decreases in stomatal aperture hence increases in the resistance to CO_2 diffusion (Bar-Tsur et al., 1985; Moon et al., 1987; Tenhunen et al., 1984). Yet, contrasting results on stomatal response to high temperature have also been reported on *Prunus domestica* (Even-Chen et al., 1981), *Vicia*

Table 4-3. The changes in photosynthetic rate and stomatal conductance for impatiens cultivars 'Dazzler White' and 'S. E. Red Velvet' after being held at temperature regimes of 38/30 or 28/20°C for 2 weeks.

Temperature treatment (°C) (day/night)	Photosynthesis rate ($\mu mol/m^2/sec$)		Stomatal conductance (cm/sec)	
	Dazzler White	S.E. Red Velvet	Dazzler White	S.E. Red Velvet
38/30	14.6	9.7	1.41	1.23
28/20	18.7	19.8	1.20	1.24

Temperature	.0001	.2717
Cultivar	.0715	.0145
Temperature x cultivar	.0765	.0149

faba (Rogers et al., 1981) and *Vitis vinifera* (Sepúlveda and Kliewer, 1986b), where stomata opened with increasing temperature. In the present study, nonstomatal inhibition of photosynthesis appears to occur in impatiens, since stomatal conductance was not affected by high temperature treatment. The nonstomatal inhibition could be either at the mesophyll cell or chloroplast levels. Decreases in CO_2 solubility and increases in O_2/CO_2 ratio at high temperature may cause increases in mesophyll resistance of C3 plants (Ku and Edwards, 1977; Laing et al., 1974; Lawlor, 1979). Decreases in RuBP carboxylase activity and injury to photosystem II and thylakoid membrane can be causes of more direct effects of high temperature inhibition on photosynthesis (Hall and Keys, 1983; Kobza and Edwards, 1987; Markus et al., 1981; Ruter, 1989).

Apparently, 'Dazzler White' is more resistant to heat stress than 'S.E. Red velvet' because the decreases in flower size and photosynthesis were greater in 'S.E. Red Velvet' than in 'Dazzler White'. The decrease in photosynthesis may indicate that there is less photoassimilate available for growth. If stress persists, the limited carbon supply may not meet the demand of active growth in flower buds, and ultimately affect flower development.

CHAPTER 5
HIGH TEMPERATURE EFFECTS ON TRANSPIRATION AND WATER STATUS FOR TWO *IMPATIENS WALLERANA* CULTIVARS

Introduction

Heat stress is often accompanied by water stress (Levitt, 1980; Lawlor, 1979). Excessive water loss due to increased stomatal aperture and vapor pressure gradient between mesophyll cells and ambient air has been reported on crops grown under high temperatures (Hale and Orcutt, 1983; Kramer, 1983). Transpiration is driven by the vapor pressure gradient, and its rate is controlled by stomatal aperture and the resistance along the evaporation pathway (Wuenscher and Kozlowski, 1971). Genetic differences exist in the response of stomata to high temperatures. Some plants may close stomata when temperatures are higher than optimal (Imbamba and Tieszen, 1977), while other plants do not close stomata until the guard cells are damaged (Rogers et al., 1981).

Water stress has been pointed out to alter numerous growth and metabolic processes (Eastin et al., 1983; Hanson and Hitz, 1982; Hsiao, 1973; Lawlor, 1979; Turner and Burch, 1982). Smaller cell size and decreased organ sizes have been observed on plants subjected to water stress (Gilbertz, 1984; Manning et al. 1977; Quarrie and Jones, 1977). Cell expansion is the plant processes most sensitive to water stress (Hsiao, 1973). Mild stress may decrease cell expansion and leaf elongation (Boyer, 1970; Takami et al., 1981; Westgate and Boyer, 1985). Our previous studies showed that flower size decreased significantly within 1 to 2 days of exposure to high temperature, possibly due to changes in water status during high-temperature stress. The objectives of this study were to determine the temperature effect on transpiration and the water

potential change within the leaves and flower tissues, so as to clarify the interrelationships among temperature, water status, and flower size change.

Materials and Methods

Uniform seedlings of 'Dazzler White' and 'Super Elfin Red Velvet' were obtained as plugs from Natural Beauty of Florida in Apopka, Florida, and planted in 10-cm pots in Vergro Klay Mix. The cultural practices were the same as in the previous experiments.

Experiment 1. Temperature treatments and environmental conditions were the same as those in Experiment 1 in Chapter 4. Seedlings were planted on 20 June 1988. After 3 weeks, plants were moved into three day/night temperature regimes to start the treatments on 10 July 1988. Abaxial surface transpiration rates and diffusive resistance were determined on the first fully expanded leaf using a steady state porometer (LI-COR Model 1600, LI-COR Inc., Lincoln, NE 68504) after the plants had been held in temperature treatments for 1 week. Measurements were recorded between 1200 and 1300 HRS EST. The experiment was in a split-plot design with four replicates and two plants per experimental unit.

Experiment 2. Plants were grown in a fiberglass covered greenhouse with a fan and pad cooling system until the plants reached a size of about 12 cm in height and 15 cm in width. Greenhouse temperatures ranged from a maximum day of 32°C to a minimum night of 18°C. The plants were then moved into a 6m x 6m glasshouse with day/night temperatures of 28/20°C. After 3 days, the plants were placed at 38/30, 33/25, or 28/20°C on 14 November 1989. Temperature fluctuation was 1.5°C above or below the set temperature. Day temperatures were set from 1000 to 1600 HRS EST. The 28/20°C treatment was considered as an optimal control temperature. Average midday light level on a clear day was 900 μmol m^{-2} sec^{-1}. Plants were watered as needed to prevent wilting. To avoid root zone heating by direct sunlight, each individual plant was placed

inside a 15-cm pot. The experiment was in a split-plot design with three replicates and three plants per experimental unit.

Leaf water potential components, and leaf and petal relative water content (RWC) were determined between 1200 and 1300 HRS EST on days 1, 2, 4, and 8. A pressure chamber and thermocouple psychrometers were used to measure water potential, while only the latter was used for osmotic potential and turgor potential determination. For pressure chamber measurements, a lateral shoot with stem diameter of about 0.3 cm was excised from plants and quickly placed in a humidified plastic bag to prevent further desiccation (Bennett et al., 1986). The xylem potential of the shoot was then determined by increasing the chamber pressure at <1.5 MPa per min.

Immediately after the pressure chamber reading, four 1-cm diameter leaf discs were excised from the two youngest mature leaves on two other shoots and rapidly enclosed in a thermocouple psychrometer chamber. The chambers were placed in a barrel with water temperature at about 30°C until transported to the laboratory within 30 min, and then were placed in a thermostatically controlled water bath at 30°C. Leaf water potential was determined with a Wescor Model HR-33T microvoltmeter after 5 hr of equilibration. The tissue was then frozen, thawed, and re-equilibrated for 5 hr. The output was determined again to obtain osmotic potential. Turgor potential was calculated as the difference of the leaf water potential and osmotic potential.

For leaf RWC, two leaf discs with diameters of 1.2 cm were excised from the leaves opposite to the leaves used for psychrometer measurements. For flower petal RWC, three petals were collected from each plant. The samples were immediately placed in a cool, humidified chamber and weighed for fresh weight within 30 min. Then the samples were floated on deionized water for 6 hr, reweighed, and oven-dried at 70°C for 24 hr. RWC was calculated as:

$$\%RWC = [(\text{Fresh weight} - \text{Dry weight})/(\text{Turgor weight} - \text{Dry weight})] \times 100$$

The entire experiment was repeated two more times on 23 November and 1 December 1989.

Results and Discussion

Transpiration rates and leaf diffusive resistances of 'Dazzler White' and 'S.E. Red Velvet' responded similarly to increasing temperatures (Table 5-1). For both cultivars, transpiration rate was lowest at 28/20°C and increased significantly as temperature was raised to 33/26°C. However, there was little change in transpiration when temperature increased from 33/26 to 39/31°C. Temperature effects on leaf diffusive resistance were somewhat different from that on transpiration. Leaf diffusive resistances of both cultivars decreased as temperature was increased from 28/20 to 33/26°C, followed by an increase as temperature raised to 39/31°C. The leaf diffusive resistance changes in 'Dazzler White' were significant between 33/26 and 39/31°C only. There was no cultivar effect or temperature and cultivar interactions detected.

Transpiration is controlled by diffusive resistance, which consists of mesophyll resistance and stomatal resistance. Transpiration is driven by the vapor pressure gradient between mesophyll cell surface and ambient air. In this study, although the relative humidity was maintained at the similar level, the vapor pressure gradient could be twice as great at 39°C as at 28°C, thus explaining the significant increase in transpiration and small changes in leaf diffusive resistance. Similar results have been reported on other crops (Hofstra and Hesketh, 1969; Neilson and Jarvis, 1975). The diffusive resistance did not show a significant difference between 28 and 39°C. This result is in agreement with previous data determined with the Li-Cor 6200 in Experiment 1, Chapter 4. Kaufmann (1982) proposed that stomatal function is controlled primarily by light intensity and absolute humidity difference from leaf to air and secondarily by temperature at extreme levels.

Water potentials in 'Dazzler White' were normally lower than those in 'S.E. Red Velvet'. Xylem water potentials determined with the pressure chamber generally decreased as temperature increased (Table 5-2). There was an interaction between temperature and time. The xylem water potential for plants in 38/30°C was significantly lower than for plants in the other

Table 5-1. Midday transpiration rate and leaf diffusive resistance for impatiens cultivars 'Dazzler White' and 'S. E. Red Velvet' after being held at temperature regimes of 39/31, 33/26, or 28/20°C for 7 days.

Temperature treatment (°C) (day/night)	Transpiration rate ($\mu g/cm^2/sec$)		Leaf diffusive resistance (sec/cm)	
	Dazzler White	S.E. Red Velvet	Dazzler White	S.E Red Velvet
39/31	30.2	29.9	0.59	0.61
33/26	31.1	28.3	0.37	0.45
28/20	25.2	23.9	0.42	0.49

Temperature	.0005	.0002
Cultivar	.1491	.1422
Temperature x cultivar	.6152	.8628

Table 5-2. Xylem water potentials determined by the pressure chamber method for impatiens cultivars 'Dazzler White' and 'S.E. Red Velvet' after being held at day/night temperatures of 38/30, 33/25, or 28/20°C for 1, 2, 4, or 8 days.

Temperature treatment (°C) (day/night)	Cultivar	Water potential (MPa)			
		Day 1	Day 2	Day 4	Day 8
38/30	Dazzler White	-0.45	-0.60	-0.54	-0.53
33/25	Dazzler White	-0.41	-0.47	-0.41	-0.44
28/20	Dazzler White	-0.34	-0.40	-0.37	-0.38
38/30	S.E. Red Velvet	-0.42	-0.52	-0.50	-0.48
33/25	S.E. Red Velvet	-0.39	-0.45	-0.39	-0.40
28/20	S.E. Red Velvet	-0.34	-0.38	-0.33	-0.36

Temperature	.0001
Cultivar	.0001
Day	.0001
Temperature x cultivar	.1086
Temperature x day	.0055
Cultivar x day	.6537
Temperature x cultivar x day	.8939

temperature regimes. Xylem water potentials for plants in 28/20°C were fairly constant throughout the experiment and ranged from -0.33 to -0.40 MPa for both cultivars, while plants at 38/30°C were below -0.42 MPa. The leaf water potentials measured with thermocouple psychrometer for both cultivars showed similar trends as found in pressure chamber readings (data not shown).

High transpiration caused excessive water loss which resulted in subsequent lower leaf water potential for the plants at higher temperature treatments. The difference in water status possibly could have also been due to reduced water absorption by the roots. The amount of water absorption by roots is not only dependent on the availability of water in the soil, but also on the amount of roots, age of root at the absorbing zone, and the rate of new root growth (Hale and Orecutt, 1987). Suberization of root endodermic cells increases the root resistance to water absorption. Most evidence indicates that water is preferentially absorbed by the root section immediately behind the zone of elongation where impermeable Casparian strips have not formed and endodermic cells have not suberized (Turner and Burch, 1982). As suberization occurs, the water uptake by roots may be reduced to about 10% of the maximum (Clarkson, 1984). Soil temperature at 20 to 30°C is optimal for root growth of most mesophytes (Kramer, 1983; Gliński and Lipiec, 1990). There was little root growth observed in *Phaseolus vulgaris* (Brouwer, 1964) and tomato (Hurewitz and Janes, 1983), and water stress developed due to reduced water absorption (Brouwer, 1964). Kramer (1969) pointed out that high soil temperature not only limited root growth but also induced cell wall suberization which made them less permeable to water. Our unpublished data shows that high root temperature at 38°C reduced root growth compared to 28°C. In this experiment, measured root temperatures were near 39°C. In this study, it is possible that high transpiration coupled with reduced water uptake caused lower plant water potentials at the higher temperatures.

Osmotic potentials determined by the psychrometric method demonstrated treatment effect similar to those in xylem water potential measurements (data not shown). However, the data were more variable and only the temperature effects were significant. Turgor potentials were

lowest in plants at the highest temperature and coincided with the observed midday wilt for some plants in the highest temperature treatments.

RWC data determined for leaves (Table 5-3) and petals (Table 5-4) supports the fact that high temperatures induced plant water deficit. Cultivar effects and interactions were not significant. At any temperature regime, flower petals always had higher water content than did leaves. The average RWC at control temperature was about 87% for leaves and 91% for petals. At 38/30°C, the drop in RWC was about 4% in petals and 7% in leaves. The greater drop in RWC for leaves than for petals is readily explainable by higher transpiration in leaves. Microscopic evaluation indicated that there were no stomata on petals. The decreases in petal RWC under high temperature may possibly result from lack of water supply due to low xylem water potential, or it may be due to the petals losing water to xylem and leaves as suggested by Nonami and Boyer(1989). Water in different tissues can be freely re-distributed within a plant (Kozlowski, 1972; Matyssek et al., 1988). The movement of water is dependent on the water potential gradient for different tissues. Diurnal shrinkage in fruit sizes due to high midday transpiration has been reported on apples (Tromp, 1984) and Calamondin orange (Chaney and Kozlowski, 1971).

Turgor potential is the one water potential component that is most important to cell expansion (Kirkham et al., 1972; Takami et al., 1981). The process of flower opening is the result of petal elongation accompanied by cell expansion and cell elongation (Goldschmidt, 1968; Jernstedt, 1980; Koning, 1984). Cell expansion and elongation require import of ions and carbohydrate for cell wall synthesis and osmotic adjustment, and involve continuous influx of water to increase cell volume (Aspinall, 1986; Stead and Moore, 1977). Although the mechanism of causing lower water potentials within the growing region is still in debate, the general concept that water potential gradient is the driving force for water influx and cell expansion has been established (Cutler et al., 1980; Matyssek et al., 1988; Michelena and Boyer, 1982; Molz, 1978; Nonami and Boyer, 1989; Westgate and Boyer, 1985). However, when water stress develops, the gradients in water potential extending from xylem to the enlarging tissues were reduced due to

Table 5-3. Leaf relative water content (RWC) for impatiens cultivars 'Dazzler White' and 'S.E. Red Velvet' after being held at day/night temperatures of 38/30, 33/25, or 28/20°C for 1, 2, 4, or 8 days.

Temperature treatment (°C) (day/night)	Cultivar	Relative water content (%)			
		Day 1	Day 2	Day 4	Day 8
38/30	Dazzler White	81.8	80.7	79.4	78.0
33/25	Dazzler White	86.3	82.7	84.0	82.5
28/20	Dazzler White	88.8	85.0	86.7	86.9
38/30	S.E. Red Velvet	83.2	82.6	80.5	78.9
33/25	S.E. Red Velvet	85.6	83.7	84.8	83.7
28/20	S.E. Red Velvet	89.3	85.7	87.0	88.5

Temperature	.0079
Cultivar	.0775
Day	.0007
Temperature x cultivar	.8231
Temperature x day	.1013
Cultivar x day	.9243
Temperature x cultivar x day	.9944

Table 5-4. Petal relative water content (RWC) for impatiens cultivars 'Dazzler White' and 'S.E. Red Velvet' after being held at day/night temperatures of 38/30, 33/25, or 28/20°C for 1, 2, 4, or 8 days.

Temperature treatment (°C) (day/night)	Cultivar	Relative water content (%)			
		Day 1	Day 2	Day 4	Day 8
38/30	Dazzler White	86.2	88.3	87.1	85.7
33/25	Dazzler White	90.3	88.9	90.2	90.5
28/20	Dazzler White	93.2	91.0	93.6	92.0
38/30	S.E. Red Velvet	90.1	85.5	87.8	85.8
33/25	S.E. Red Velvet	92.0	91.4	92.4	88.3
28/20	S.E. Red Velvet	92.6	91.3	91.7	89.2

Temperature	.0065
Cultivar	.8567
Day	.0136
Temperature x cultivar	.1368
Temperature x day	.9944
Cultivar x day	.1259
Temperature x cultivar x day	.1738

the decrease in xylem water potentials (Nonami and Boyer, 1989; Westgate and Boyer, 1985). Therefore, the movement of water into the tissue for cell enlargement decreased. In this study, high temperature tended to decrease water potential components and RWC. The decrease in turgor potential found in psychrometer measurements is in agreement with the observation that some plants showed wilt symptoms in high temperature treatments.

The general concept that water stress decreases cell expansion and cell sizes has been demonstrated on many different plants (Barlow, 1986; Bunce, 1978; Cutler et al., 1977; Hsiao, 1973; Matsuda and Riazi, 1981). In sunflower, rates of leaf enlargement have been reported to decrease at leaf water potentials below -0.2 MPa and to be stopped at -0.4 MPa (Boyer, 1970). Similar results have been reported by Takami et al. (1981). More evidence is provided by the previous reports that plants subjected to water deficit had significantly smaller leaf area (Cutler At root temperature of 35°C or higher, et al., 1977) while the cell index (number of cells per unit of area) of leaf epidermis was much greater (Ordin, 1966). The reduction in cell size under the condition of water stress is considered an adjustment process of permitting a lower osmotic potential, hence increased capacity for turgor maintenance (Culter et al., 1977). This may further explain why the decrease in turgor as observed in high temperature treatments was less significant than those in water potential and osmotic potential. Water stress has also been reported to decrease plant sizes and dry weight in *Impatiens wallerana* (Martens, 1988). Based on the above findings and the data presented here, we conclude that the quick decrease in flower size during high temperature treatment was mainly due to the high temperature induced water stress. The water stress effect on flower development may originate from the change in water potential gradient between xylem and developing flowers because the RWC decreased more in leaf than in flower petals.

CHAPTER 6
SUPRAOPTIMAL TEMPERATURE EFFECTS ON DEVELOPING FLOWERS OF IMPATIENS: ^{14}C-ASSIMILATE PARTITIONING, CARBOHYDRATE LEVELS, AND INVERTASE ACTIVITIES

Introduction

Young leaves and developing flower buds are strong sinks competing for available photoassimilate and other nutrients for rapid development. The growth of plant tissues involves two phases: 1) cell division, which ceases at an early stage and occupies only a relatively short period of the total development time. And 2) cell enlargement, which is accompanied by a continuous import of photoassimilates and nutrients for synthesis of cell wall and plasma constituents and influx of water for cell expansion. Plant growth in size is contributed to cell expansion and elongation which are mostly the results of the increases in cell water content (Matyssek et al, 1988; Nonami and Boyer, 1989).

Either water deficit (Berüter, 1989; Brevedan and Hodeges, 1973; Huber et al., 1984; Plant and Reinhold, 1965; Vassey and Sharkey, 1989) or high-temperature stress (El Ahmadi and Stevens, 1979; Harris and Jeffcoat, 1974; Ruter, 1989; Sepúlveda et al., 1986; Shishido et al., 1987; Squire, 1989; Wardlaw et al., 1980) may alter assimilate partitioning among different plant tissues. At higher temperatures, vegetative growth is favored (Hughes and Cockshull, 1972; Whealy, 1987) and more photoassimilate is transported to young leaves at the expense of flower buds (Dinar et al., 1983). Changes in the level of available assimilates affects reproductive growth, also (Abdul and Harris, 1978; Kinet, 1977; Morris and Arthur, 1984a). However, altering the availability of photosynthate by defoliation or by partial grain removal with wheat grain did not

prevent the reduction in grain dry weight due to high temperature (30/25°C, day/night) (Wardlaw et al., 1980). The results suggested that temperature effect on grain filling did not result from an effect of photosynthate availability, but rather occurred within or close to the sink itself.

Although invertase and sucrose synthase hydrolyze sucrose into glucose and fructose, invertase seems to play a much more important role in developing flowers (Hawker et al., 1976; Woodson and Wang, 1987). The hexose from sucrose hydrolysis is either transformed into starch as reserves or further used by cells for respiration, structures, and other metabolism (Berüter, 1989; Ho, 1986; Nichols and Ho, 1979; Whiting, 1970). Sucrose hydrolysis by acid invertase may be the process that regulates the assimilate unloading and uptake by sink tissues (Eschrich, 1980; Harris and Jeffcoat, 1974; Walker et al., 1978). High invertase activities are usually observed on developing sink tissues with rapid cell enlargement (Howard and Witham, 1983; Morris and Arthur, 1984a; 1984b; 1985a; Poovaiah and Veluthambi, 1985). However, high temperatures have been reported to inhibit invertase activity, and, consequently, cause accumulation of sucrose in sink tissues (Dinar and Rudich, 1985b).

Carbohydrate level is an important factor for flower development. It is affected by assimilate partitioning and its further metabolism is associated with invertase activity. Low carbohydrate levels in flower buds have been reported to be associated with the reduced flower sizes and poor fruit set in tomato plants subjected to high temperature stress (Satti and Oebker, 1986). In the past, pulse-chase labelling with $^{14}CO_2$ has been applied to the study of assimilate partitioning within a plant (Koch and Schrader, 1984; Barrett and Amling, 1978). The objectives of this study were to use this pulse-chase technique together with carbohydrate analysis to determine whether the decrease in flower size, as previously observed with high temperatures is related to a change in carbohydrate levels and/or to the factors that may change assimilate partitioning.

Materials and Methods

Uniform seedlings of 'Dazzler White' and 'Super Elfin Red Velvet' were obtained as plugs from Natural Beauty of Florida in Apopka, Florida. Seedlings were planted in 10-cm pots in Vergro Klay Mix. The cultural practices were the same as in the previous experiments. All temperature treatments were conducted in three 6m x 6m glasshouses, in which the day/night temperatures were set at 38/30, 33/25, or 28/20°C. Experiments were in a split-plot design, with two plants per experimental unit. There were three replicates in Experiment 1 and 3, and four replicates in Experiment 2.

Experiment 1. Three weeks after planting, plants were moved into the temperature treatments on 17 March 1990. After being held in the treatment for 10 days, $^{14}CO_2$ labelling was performed. The youngest fully expanded leaf on the main stem was sealed in a 15 x 10 cm zipper-seal sample bag in which a 1.5-ml microcentrifuge tube was taped upward. After a leak test, 0.37 MBq [^{14}C]-$NaHCO_3$ (specific activity 2.16 GBq mmol^{-1}) was injected into the tube as the source of $^{14}CO_2$, which was released by adding 40 µl of 20% H_2SO_4. The injection hole was immediately sealed. Cool air or running tap water was applied to the bag surface to avoid excessive heat build up in the bag. Labelling was conducted between 1100 and 1200 HRS EST. After 20 min, the bags were removed and the plants were left in the same temperature regimes for an additional 24 hr. The leaf labelled with $^{14}CO_2$ was considered as the 'source leaf' for all exported ^{14}C-assimilate.

$^{14}CO_2$-labelled plants were separated into flower buds, leaves above and below the labelled leaf, stem, and other shoots. The stem was the shoot containing the labelled leaf. All shoots divided from the main stem were combined as other branches, which included leaves and buds. Samples were frozen in liquid nitrogen, chopped and boiled in 80% (v/v) ethanol for 20 min and then ground in a Vitis homogenizer (The Vitis Company, Inc., Gardiner, NY). Ethanol soluble material was separated from ethanol insoluble material by filtering the ground samples through

a fiberglass filter paper and thoroughly washing with ethanol. One hundred micro liters of the ethanol soluble samples was added to 10 ml of scintillant (ScintiVerse II, Fisher Scientific, Orlando, FL) and 3 ml of distilled H_2O. Ethanol insoluble solid was vacuum dried at room temperature, weighed, and re-ground before adding 50 mg of sample to the same scintillant. All samples were well mixed and held at room temperature for 48 hr before counting. Radioactivity was determined with a LKB 1214 liquid scintillation counter (LKB Wallac, Turku, Finland). The radioactivity in the flower buds, leaves above the source leaf, leaves below the source leaf, stems, and shoots was expressed as percentage of the total in above ground tissues excluding the labelled leaf. The experiment was repeated two times on 26 March and 7 April 1990. Each repeat was considered as a replicate.

Experiment 2. Samples for invertase assay were collected from plants that had been grown in the three temperature regimes (as in Experiment 1) for 10 days. From each plant, 0.3 g of flower petals and young leaves were collected, immediately frozen in liquid N_2, and kept at -80°C for future use. The flower petals were collected from young flower buds (YFB), smaller than 4 mm in length, and the young leaves (YL) were the expanding leaves with area less than 20% that of fully expanded leaves. For enzyme assay, tissues were ground in liquid N_2 with a mortar and pestle, then transferred in 3 ml of 200 mM Hepes buffer (pH 7.5), with 1 mM DTT, 5 mM $MgCl_2$, 1 mM EGTA, 10 mM Na-Ascorbate, and 5% PVPP. Homogenate was filtered through cheesecloth, rinsed with extraction buffer, and centrifuged at 20000 g for 10 min. The supernatants were dialyzed against 5 mM potassium phosphate buffer (pH7.5) containing 1 mM DTT for 24 hr. Cell wall material for assays of insoluble invertase was washed with 10 ml diluted extraction buffer. All preparation steps were conducted at 2-4°C. Since the acid invertase activity was the primary objective in this experiment, no effort was made to test alkaline invertase.

Invertase activity was determined by adding 70 µl of enzyme extract to 10 µl H_2O and 10 µl 0.2 M acetate buffer at 37°C for 10 min. The reaction was started by adding 10 µl of 1 M sucrose to the solution and terminated by boiling the samples at 100°C for 60 sec. Reaction

mixture containing heat-denatured enzyme were used as background. Glucose resulting from sucrose hydrolyzation was determined with a glucose diagnostic kit (Procedure No. 510, Sigma). Protein content in the desalted tissue extract was determined by the Bio-Rad dye binding procedure using bovine serum albumin as standard.

Experiment 3. After being held in temperature treatments for 10 days, samples of YFB, mature buds (flower buds larger than 8 mm), YL were collected from each plant and immediately frozen in liquid nitrogen, freeze dried at -40°C, and then finely ground. For carbohydrate determination, 0.1 g of the dry samples were extracted with 5 ml of 80% (v/v) ethanol in a shaking water bath for 30 min at 80°C. After extraction, the samples were centrifuged at 10000x g for 10 min, the supernatants were decanted and the pellets were extracted two more times following the same procedures. The supernatants were combined, and chloroform and water were added to bring the final ethanol:chloroform:water ratio to 10:6:5. They were held in a refrigerator over night. Lipids and pigments in the samples were subsequently removed in the chloroform layer. The aqueous-ethanol layer was evaporated to dryness, and resuspended in a known volume of HPLC-grade H_2O, followed by passing through a 45 μm nylon syringe filter. Samples were analyzed for soluble sugars with a Bio-Rad and HPLC system (Richmond, CA) using a calcium-form cation exchange column (HPX-87C, Bio-Rad). The column temperature was maintained at 85°C and the flow rate of water was 0.6 ml min^{-1}.

The ethanol insoluble materials were added with 2 ml of 0.1 M acetate buffer (pH 5.6), and placed in 85°C for 30 min in order to swell starch grain. After the samples cooled, 3 ml of enzyme solution was added and the samples were incubated in a shaking water bath for 24 hr at 37°C. The enzyme solution was 0.1M acetate buffer (pH 5.6) containing alpha-amylase (50 units ml^{-1}), amyloglucosidase (5 units ml^{-1}), and 0.1 mM $CaCl_2$. After incubation, samples were centrifuged at 12000x g for 20 min, supernatants decanted and adjusted for volume. The glucose concentration digested from starch was determined enzymatically with a glucose diagnostic kit as mentioned in Experiment 2.

Results and Discussion

Experiment 1. Temperature significantly affected the percentage of ^{14}C-assimilate partitioned among different above-ground tissues (Table 6-1). At all temperature treatments, flower buds were the strongest sink tissues and accumulated 38 to 68% of total exported ^{14}C recovered in both cultivars. This is similar to the reports for *Phaseolus vulgaris* where about 65% of the currently-fixed carbon was partitioned to the reproductive parts during the flowering period (Geiger and Shieh, 1988). The percentage of ^{14}C transported into the flower buds of 'S.E. Red Velvet' decreased as temperature increased while that of 'Dazzler White' did not show significant difference. In 'S.E. Red Velvet', the ^{14}C levels in stems and lateral shoots were approximately twice as high at 38/30 compared to 28/20°C. Apparently, at high temperatures, the ^{14}C-assimilate shifted from the flower buds of 'S.E. Red Velvet' was found in stems and other shoots. There was an interaction between cultivars and temperature for the amount of ^{14}C exported to the branch shoot. In 'S.E. Red Velvet', the percent total ^{14}C recovered from lateral shoots increased with temperature, but in 'Dazzler White' there was about 10 percent more at the middle temperature than in either 38/30 or 28/20°C. The reason for this difference in 'Dazzler White' is not clear. The movement of ^{14}C-assimilate from one shoot to another seems a common phenomenon in many plants and is affected by environmental conditions (Ryle and Powell, 1972).

Assimilate partitioning within a plant is affected by temperature and water stress. Several studies have demonstrated that the effect of water stress on assimilate translocation was not limited to the phloem transport pathway itself (Sung and Krieg, 1979; Wardlaw, 1967). However, the translocation velocity in the sieve elements of cacao was reduced by water stress (Deng et al., 1990). In *Ricinus communis*, Smith and Milburn (1980) reported about 50% higher solute concentration in phloem-sap of plants under water stress than in controls although the rate of phloem transport was not changed. They concluded that the increase in solute concentration in the phloem is necessary to maintain positive turgor for pressure flow in phloem transport. In

Table 6-1. Changes in ^{14}C-assimilate partitioning among different plant parts for impatiens cultivar 'Dazzler White' and 'S.E. Red Velvet' after being held at day/night temperature of 38/30, 33/25, or 28/20°C for 10 days. (%)[z]

Temperature treatment (°C) (day/night)	Cultivar	Flower buds	Leaves[y] above source leaf	Leaves below source leaf	Stem	Other[x] shoots
38/30	Dazzler White	54.8	1.7	0.6	22.8	20.2
33/25	Dazzler White	43.3	2.6	1.7	22.3	30.1
28/20	Dazzler White	55.8	2.3	0.6	21.9	19.4
38/30	S.E. Red Velvet	38.1	2.5	1.9	28.2	29.3
33/25	S.E. Red Velvet	49.4	3.2	0.8	20.8	25.8
28/20	S.E. Red Velvet	68.7	1.4	0.6	15.4	13.9
Temperature		.0001	.0780	.5032	.0243	.0064
Cultivar		.7743	.6922	.7669	.5313	.9104
Temperature x cultivar		.0003	.2121	.2052	.0063	.0044

[z] Percentage of the total ^{14}C recovered in the above ground tissues excluding the labelled source leaf.
[y] Source leaf was the leaf labelled with $^{14}CO_2$.
[x] All lateral shoots divided from the main stem were combined as other shoots, which includes leaves and buds.

Chapter 5, it was pointed out that the plants in high temperature were subjected to some degree of water stress. This is in agreement with the observation that some plants showed wilt symptoms in the high temperature treatments. The increase in ^{14}C recovered from the stems of 'S.E. Red Velvet' in higher temperature as observed in this study could possibly be due to high temperature induced water stress. Furthermore, callose formed in sieve plates of plants subjected to heat stress has been observed in cotton (Dinar et al., 1983; McNairn, 1972). Milburn and Kallarackal (1989) postulated that this callose formation might constrict the sieve tube pore and reduce phloem translocation. Therefore more labelled carbon was retained in the stems. However, the response of translocation rate to water stress was significantly affected by different genotypes (Sung and Krieg, 1979), and the partitioning could also be altered by the differential sensitivity of plant tissue to low water potential (Westgate and Boyer, 1985). This may explain why the percent recovered ^{14}C from the stems of 'Dazzler White' was not changed, while that of 'S.E. Red Velvet' was.

The percent total ^{14}C recovered from the leaves above or below the labelling leaf was not significantly different among temperature treatments or cultivars. There was only a small percent of ^{14}C-assimilate transported to the leaves above the source leaf. In tomato grown in supraoptimal temperature, more photoassimilate was found transported to YL, which resulted in lower carbohydrate levels in flower buds and poor fruit set (Dinar and Rudich, 1985a). Similar results were reported for grapevines (Sepúlveda et al., 1986). In this study, the YL were a minor sink and did not compete strongly for the available ^{14}C-assimilate even in the highest temperature.

Experiment 2. High temperature affected invertase activity but differences in cultivar response were observed (Table 6-2). In 'S.E. Red Velvet', invertase activity decreased 34 to 50% in flower petals and 40 to 49% in YL at 33/25 and 38/30°C compared to the 28/20°C treatment. However, in the heat tolerant 'Dazzler White', there was only a small change in invertase activity in either flower petals or in YL. Similar inhibition of invertase activity by high temperature has

Table 6-2. Invertase activity in flower petals and young leaves of impatiens cultivars 'Dazzler White' and 'S. E. Red Velvet' after being held at temperature regimes of 38/30 or 28/20°C for 10 days. (μmol glucose/mg protein/ hr)

Temperature treatment (°C) (day/night)	Flower petals[z]		Young leaves[y]	
	Dazzler White	S.E. Red Velvet	Dazzler White	S.E Red Velvet
38/30	7.7	13.6	3.0	6.5
33/25	8.3	16.7	3.8	7.5
28/20	9.0	24.7	4.7	12.6
Temperature	.0013		.0001	
Cultivar	.0001		.0001	
Temperature x cultivar	.0003		.0017	

[z] Petals were collected from the flower buds smaller than 4 mm in length.
[y] Leaves with area less than 20% of that of fully expanded leaves.

been reported for tomato (Dinar and Rudich, 1985a; 1985b). In contrast to Dinar et al.'s report that higher invertase activity was found in heat tolerant cultivars than in heat sensitive cultivars under high temperature stress, we found that 'Dazzler White', the heat tolerant cultivar, had lower invertase activity than did 'S.E. Red Velvet'. The reason for these opposite results is not clear. Nevertheless, it could be possible that 1) there was some sucrose synthase activity in the flower petals of 'Dazzler White' although invertase is predominant in the flower buds of most plants; or 2) like the problem encountered by Madore (1990), high levels of hydrolytic and other enzymes may interfere with the assay activity. There was no insoluble invertase activity detected in cell wall fractions.

Experiment 3. Substantial levels of sucrose were found in all tissues of 'Dazzler White' and 'S.E. Red Velvet' (Table 6-3). There was no interaction between temperature and cultivar. As temperature increased, the sucrose levels in YFB and in YL increased consistently, while there was a small change in mature flower buds. Generally, 'Dazzler White' accumulated more sucrose in YFB than did 'S.E. Red Velvet'. For both cultivars, YFB contained more sucrose than did mature buds. Heat stress causing accumulation of sucrose in young developing tissues has also been reported for grapevine (Sepúlveda and Kliewer, 1986a) and tomato (Dinar and Rudich, 1985a; Satti and Oebker, 1986).

Temperature treatment did not change the glucose level in YFB and YL for either cultivar although the level was lower in 'S.E. Red Velvet' than in 'Dazzler White' (Table 6-4). However, the glucose level in mature buds was significantly lower in 38/30°C than in the other two temperature treatments. No significant difference in fructose was observed due to temperature or cultivar effect in all three tested plant tissues.

The starch content in YFB was lowest at the highest temperature for both cultivars; the difference was greater in 'S.E. Red Velvet' than in 'Dazzler White' (Table 6-5). In mature buds, temperature did not affect the starch content in 'S.E. Red Velvet', but in 'Dazzler White' the highest level was in the 28/20 treatment. Temperature treatments had little effect on the starch

Table 6-3. Sucrose content in the flower buds and young leaves of impatiens cultivar 'Dazzler White' and 'S.E. Red Velvet' after being held at day/night temperature of 38/30, 33/25, or 28/20°C for 10 days. (mg/100 mg dry weight)

Temperature treatment (°C) (day/night)	Cultivar	Young flower buds[z]	Mature flower buds[y]	Young leaves[x]
38/30	Dazzler White	5.60	3.01	4.47
33/25	Dazzler White	3.76	2.53	2.73
28/20	Dazzler White	3.27	2.80	2.47
38/30	S.E. Red Velvet	3.95	2.69	3.77
33/25	S.E. Red Velvet	3.22	2.49	2.79
28/20	S.E. Red Velvet	2.82	2.42	2.49
Temperature		.0028	.7806	.0131
Cultivar		.0025	.6077	.6516
Temperature x cultivar		.0570	.9510	.7325

[z] Flower buds smaller than 4 mm in length.
[y] Flower buds larger than 8mm in lenth, which were about 2 to 3 days prior to flowering.
[x] Young leaves with area less than 20% of that of fully expanded leaves.

Table 6-4. Glucose content in the flower buds and young leaves of impatiens cultivar 'Dazzler White' and 'S.E. Red Velvet' after being held at day/night temperature of 38/30, 33/25, or 28/20°C for 10 days. (mg/100 mg dry weight)

Temperature treatment (°C) (day/night)	Cultivar	Young flower buds[z]	Mature flower buds[y]	Young leaves[x]
38/30	Dazzler White	1.91	0.85	1.63
33/25	Dazzler White	1.53	2.27	1.62
28/20	Dazzler White	1.59	2.24	1.47
38/30	S.E. Red Velvet	1.19	0.45	0.98
33/25	S.E. Red Velvet	1.25	2.28	0.98
28/20	S.E. Red Velvet	1.42	2.97	0.97
Temperature		.0850	.0016	.7608
Cultivar		.0052	.6434	.0007
Temperature x cultivar		.1051	.2180	.7676

[z] Flower buds smaller than 4 mm in length.
[y] Flower buds larger than 8mm in length, which were about 2 to 3 days prior to flowering.
[x] Young leaves with area less than 20% of that of fully expanded leaves.

Table 6-5. Starch content in the flower buds and young leaves of impatiens cultivar 'Dazzler White' and 'S.E. Red Velvet' after being held at day/night temperature of 38/30, 33/25, or 28/20°C for 10 days. (mg/100 mg dry weight)

Temperature treatment (°C) (day/night)	Cultivar	Young flower buds[z]	Mature flower buds[y]	Young leaves[x]
38/30	Dazzler White	2.63	1.27	4.68
33/25	Dazzler White	3.38	1.24	4.36
28/20	Dazzler White	2.92	2.15	4.60
38/30	S.E. Red Velvet	1.81	1.40	4.15
33/25	S.E. Red Velvet	3.05	1.43	3.91
28/20	S.E. Red Velvet	3.18	1.30	3.34
Temperature		.0001	.0069	.1525
Cultivar		.0256	.0463	.0367
Temperature x cultivar		.0130	.0015	.4722

[z] Flower buds smaller than 4 mm in length.
[y] Flower buds larger than 8 mm in length, which were about 2 to 3 days prior to flowering.
[x] Young leaves with area less than 20% of that of fully expanded leaves.

contents in YL for both cultivars. The significantly low starch content in YFB of 'S.E. Red Velvet' at the highest temperature may be a result of less carbon import as observed in $^{14}CO_2$ pulse-chase study in Experiment 1.

These results show that both starch contents and sucrose levels decreased as flower buds developed from young to mature. The hydrolysis of starch is believed to increase the sugar levels in developing cells. During rapid development of flower buds, more carbon is needed for metabolism and synthesis of cell walls and cell components (Cliquet et al., 1990; Kinet et al., 1985). However, under high temperature conditions, the significantly lower starch contents in young buds and extremely low glucose level in mature buds as observed in this study may limit the normal development of flowers. In developing tissues, a large proportion of imported sugar may be depleted in respiration (Ho, 1986). At the whole plant level, about 45% of photoassimilate has been demonstrated to be lost in respiration (Shishido et al., 1987) and only about 25 to 35% is used for biosynthesis (Gifford, 1986). Generally, respiration has a higher optimum temperature than other processes and increases rapidly as temperature increases (Lambers et al., 1983; Sutcliffe, 1977). As temperature increased, excessive depletion of available carbohydrate in flower buds through respiration would consequently result in low carbohydrate levels and reduced growth. In this study, if the sum of sucrose, glucose, fructose, and starch account for the majority of total non-structural carbohydrate, it decreased consistently in the mature buds for both cultivars as temperature increased from 28/20 to 38/30°C. The decrease was 16% in 'Dazzler White' and 30% in 'S.E. Red Velvet'. Apparently, under heat stress, there was a smaller carbon pool available for flower development in 'S.E. Red Velvet' than in 'Dazzler White'. This observation is in agreement with Parker's (1970) report that heat sensitive plants had higher respiration rates than heat tolerant plants under high temperature stress.

Invertase activity is generally found to be higher in the tissues with rapid cell enlargement (Morris and Arthur, 1984). Previous studies have postulated that sucrose needed to be hydrolyzed into hexoses before entering sink cells and invertase was a key enzyme in controlling

phloem unloading and carbon partitioning to sink tissues (Bennett et al., 1984; Eschrich, 1980; Russell and Morris, 1982; Walker et al., 1978). Dinar and Rudich (1985b) reported that sucrose accumulation in flower buds of tomato subjected to heat stress was mainly due to the decreased invertase activity. They also reported that the sucrose level was higher in heat sensitive cultivars with lower invertase activity than in heat tolerant cultivars. In contrast to their results, we found lower sucrose accumulation in heat sensitive 'S.E. Red Velvet' than in heat tolerant 'Dazzler White'. While phloem unloading and sucrose uptake mechanisms in sink tissues are still not clear, some evidence has shown that sucrose may enter sink cells, without breaking down, through symplast pathway via plasmadesmata (Gifford, 1984; Ho and Baker, 1982). Developing flower petals are sites of active growth with substantially developed transport systems (Fahn, 1974; Kinet et al., 1985). Therefore sucrose more likely enters petal cells through the symplastic pathway as proposed by Offler and Patric (1986). This view is supported by the fact that there is no invertase activity in cell wall residues. Furthermore, Porter et al. (1985) showed that inhibition of invertase activity by PCMBS did not affect sugar unloading and uptake in maize pedicle tissues. In this case, invertase in impatiens flower buds may play a more important role in sucrose metabolism rather than in sucrose unloading. Hence, the heat tolerant 'Dazzler White' depleted less carbohydrate as reflected in lower invertase activity therefore accumulated more sucrose. The heat sensitive cultivar 'S.E. Red Velvet' transported less current-fixed assimilate to flower buds under heat stress and probably lost more carbon during the period of flower development due to higher respiration rates. This likely resulted in more severe carbohydrate starvation under supraoptimal temperatures and limited normal development.

CHAPTER 7
SUMMARY AND CONCLUSIONS

Within the day/night temperature range of 18/24 to 34/29°C, increases in temperature generally promoted vegetative growth and reduced flower size for most of the 19 impatiens cultivars tested. The effects were more pronounced on 'S.E. Red Velvet' than 'Dazzler White'. However, temperatures of 38/30°C were later found to have an inhibitive effect on vegetative and reproductive growth for both cultivars.

The rapid reductions in flower size on plants subjected to high temperature stress may be due to water stress effects induced by high transpiration rates. Diurnal shrinkage of plant organs has been reported in several crops and is often associated with the oscillation of plant water potentials. Although the water potential in flower petals was not determined, the leaf water potentials and relative water content of leaves and petals decreased as temperature increased. The fact that the plants at 38/30°C transpired at similar rates as those in 33/25°C, but had more negative water potentials indicated that the absorption of water by the roots was impaired in the highest temperature. Leaf turgor potential determined with thermocouple psychrometers showed a general decrease as temperature increased. It is thus proposed that the lower water potential in leaves and xylem reduced the water potential gradient between water sources and the developing flowers and consequently reduced cell enlargement and final petal sizes.

Assimilate partitioning and carbohydrate metabolism may be the reason for long term effects of heat stress on flower size. Flower buds represented the strongest sink among different tissues and accumulated more currently-fixed ^{14}C-assimilate at all temperature regimes. The partitioning of assimilate to flower buds was not affected by temperature in 'Dazzler White' while in 'S.E. Red Velvet' it decreased markedly as temperature increased. There was more ^{14}C

transported to branch shoots and retained in stem tissues in 'S.E. Red Velvet'. The retention of ^{14}C-assimilate in stems may be a result of water stress. An increase in temperature inhibited invertase activity in both flower buds and young leaves. The inhibition was less in 'Dazzler White' than in 'S.E. Red Velvet'. High temperature caused decreased starch content and increased sucrose accumulation in flower buds. At late stages of flower bud development, the extremely low glucose concentration as observed in plants at 38/30°C was believed to result from low carbon reserve or excessive depletion through respiration. Changes in invertase activity in flower buds was postulated to have less effect on carbon import, but rather it is more important in sucrose metabolism within the sink tissues. In the flower buds under high temperature stress, the low levels of hexoses may result in less carbon supply for growth and consequently result in smaller flower sizes.

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BIOGRAPHICAL SKETCH

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I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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